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SIZE DIMORPHISM, MOLT STATUS, AND BODY MASS VARIATION OF PRAIRIE FALCONS NESTING IN THE SNAKE RIVER BIRDS OF PREY NATIONAL CONSERVATION AREA

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Birds face challenges in how they allocate energy during the reproductive season. Most temperate zone species do not breed and molt at the same time, presumably because of the high energy demands of these two activities (Espie et al. 1996 and citations therein). However, representatives of at least four raptor genera are known to molt during the nesting season (Schmutz and Schmutz 1975, Newton and Marquiss 1982, Schmutz 1992, Espie et al. 1996). Molt strategies vary among raptor species depending on prey abundance, migration strategies, and the relative costs of reproduction. Sexually-dimorphic raptors typically have different roles in parenting, which result in different strategies for energy allocation. Male and female Eurasian Kestrels (*Falco tinnunculus*), for example, exhibit different molt patterns and mass changes during the breeding season (Village 1990). Prairie Falcons (*Falco mexicanus*) are similar to Eurasian Kestrels in that males provide most of the prey to females and young during the first part of the nesting season (Holthuijzen 1990), but no published data exist on molt patterns or mass changes in Prairie Falcons. Reliable information about raptor molt and morphometrics has important implications for modeling energetics and for understanding the role of sexes in raising young. Such knowledge also has practical application for distinguishing sexes of raptors and for determining appropriate size limits of transmitters used for telemetry studies. In this paper, we report on morphometric characteristics useful in distinguishing sexes of Prairie Falcons captured during several breeding seasons in the Snake River Birds of Prey National Conservation Area (NCA), and we assess changes in mass and molt status through the nesting season.

METHODS

From 1978–2003, we trapped and measured adult Prairie Falcons during 12 nesting seasons in the NCA, southwest Idaho (42°50'N, 115°50'W). Falcons were trapped during several different investigations (Marzluff et al. 1997, Lehman et al. 2000, Steenhof et al. 2005), and not all measurements were recorded on all birds. In this analysis, we consider measurements and molt status recorded during 297 encounters with 279 Prairie Falcons between 1 March–20 June. Many individuals we trapped, measured, and banded were subsequently monitored through at least one nesting season as part of radiotelemetry and productivity studies (Marzluff et al. 1997, Steenhof et al. 1999, 2005). Most falcons were trapped in dho-gaza nets, using a Great Horned Owl (*Bubo virginianus*) as a lure (Bloom et al. 1992), but some birds were captured in noose carpets (Bloom 1987) placed in nest scrapes. We had no repeated measurements on individuals within the same year, but 15 individuals were measured in more than one year. The data set included 24 individuals that were initially banded as nestlings. At least nine of the females and six of the males were yearlings when they were measured, based on plumage characteristics (Steenhof 1998) or known age at banding.

We recorded masses ($N = 273$) to the nearest g with Pesola scales. We measured wing chord ($N = 269$) to the nearest mm with a ruler according to instructions in Pyle (1997:5), and we measured wingspan ($N = 184$) according to instructions in Pennycuik (1999). Tail length ($N = 99$) was measured in mm by inserting a ruler between the central rectrices at the point of their insertion. Length of exposed culmen ($N = 82$) and length of hallux claw ($N = 29$) were measured in mm with calipers according to Bortolotti's (1984) diagrams. We measured toe-pad length ($N = 201$) in mm with calipers from the distal end of the pad on the hind toe (hallux) to the distal end of the pad on the middle (third) toe, with the toes maximally extended. We considered individuals to be "molting" if we noted a missing, partially grown, or freshly grown flight feather (primary, secondary, or rectrix).

At the time of banding, investigators applied size 6 (inside diameter = 9.53 mm) bands to smaller (pre-

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Table 1. Morphometric characteristics of adult Prairie Falcons during the nesting season in southwest Idaho. Mass is measured in g; all other characteristics are mm. *t*-tests indicated that each characteristic differed significantly between the genders ($P < 0.001$).

VARIABLE	MALES				FEMALES			
	<i>N</i>	MEAN	SD	RANGE	<i>N</i>	MEAN	SD	RANGE
Mass	123	559.6	36.0	484–661	148	907.8	65.9	779–1133
Wing chord length	119	305.2	7.1	290–340	147	346.5	6.6	330–365
Wingspan	96	949.7	30.0	828–1020	88	1091.4	30.5	990–1174
Toe-pad length	97	77.4	2.1	70–82	103	90.2	2.0	84–95
Tail length	34	165.1	4.8	154–174	65	188.8	5.0	180–205
Culmen	30	18.7	0.6	17.7–20.5	52	22.4	1.0	20.2–24.8
Hallux	8	19.1	0.2	18.8–19.3	21	23.1	0.8	21.5–25

sumably male) birds and size 7A (inside diameter = 11.1 mm) bands to larger (presumably female) birds based on visual assessment of foot size. We used band sizes as preliminary designations of gender in a discriminant function analysis (DFA) of mass, wing chord, and toe-pad length ($N = 197$). We then conducted univariate *t*-tests for all other variables, based on sexes assigned by DFA. We calculated wing-loading indexes from mass and wing chord measurements, based on Mueller et al.'s (1976) formula.

We assessed molt status in relation to day of year and stage of the nesting season. We estimated median hatching dates for breeding pairs by backdating from ages of their young, as estimated from a photographic aging-key (Moritsch 1983). We assumed the last egg was laid 34 days prior to hatching (Burnham 1983). We have larger sample sizes for day of year than for nesting stage because the nesting attempts of some adults were not monitored, and some nesting attempts failed during incubation.

RESULTS

A discriminant function describing differences between the assumed sexes was significant (Wilks's Lambda = 0.04, $F_3 = 1560$, $P < 0.001$), and 100% of individuals were correctly classified based on the function derived from mass, wing chord, and toe-pad length. All characteristics we measured exhibited bimodal distributions that likely reflected different sexes, and *t*-tests indicated that each of the characteristics differed significantly between the two groups ($P < 0.001$; Table 1). Mass, toe-pad length, hallux, and tail length showed no overlap between groups. Wing chord, wingspan, and culmen showed minor overlap (Table 1). Females had a mean wing-loading index of 0.56 (range = 0.46–0.70); the index for males was 0.45 (range = 0.37–0.55).

Measurements of wing chord on the same individual in different years varied by 1–9 mm in males ($\bar{x} = 6$ mm, $N = 4$) and by 4–10 mm in females ($\bar{x} = 6$ mm, $N = 3$). The differences are likely due to measurement error rather than actual changes in wing length. Tail length was measured in consecutive years for only one individual (a male), and the measurements were identical. Masses of individuals measured in different years differed by 5–62 g in males ($\bar{x} = 29$ g, $N = 6$) and by 20–170 g in females ($\bar{x} =$

95 g, $N = 4$). The lower mass was recorded later in the nesting season for all females, but not for males.

Female masses declined significantly from the onset of incubation through brood-rearing ($r = -0.59$, $N = 92$, $P < 0.001$; Fig. 1), but male masses showed no significant change during the same period ($r = -0.27$, $N = 45$, $P = 0.07$; Fig. 1). Masses of females showed an increasing trend in the 3–4 wk prior to laying eggs. During the first 2 wk of incubation, female masses averaged 962 g ($N = 23$, $SD = 66$); by the end of the brood-rearing period, mean mass had declined 12% to 845 g ($N = 29$, $SD = 38$). The mean wing-loading index for females decreased from 0.59 early in the nesting season to 0.52 late in the nesting season.

Sixty-three percent of females ($N = 150$) and 34% of males ($N = 116$) were molting wing feathers when we trapped them. We recorded molt in females as early as 23 March and as early as 27 days prior to hatching; we recorded molt in males as early as 14 April and as early as

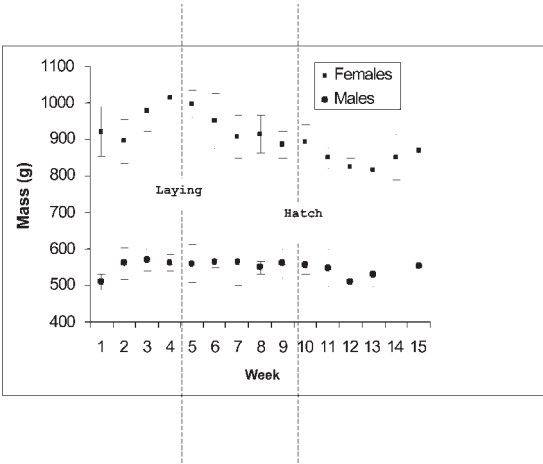


Figure 1. Masses of Prairie Falcons, by week, in relation to hatching dates of their young. Females ($N = 107$) are shown as squares. Males ($N = 74$) are shown as dots.

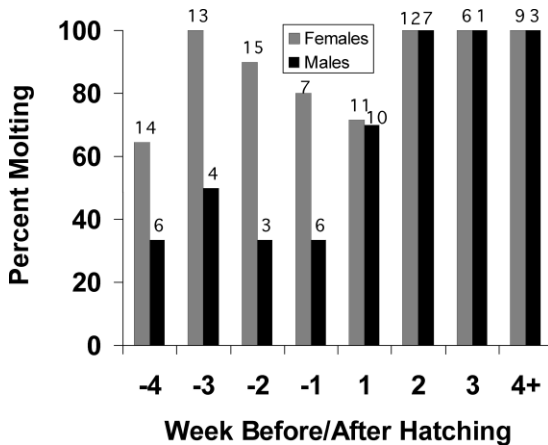


Figure 2. Percent of Prairie Falcons showing evidence of wing molt in relation to the estimated date that their clutch of eggs hatched. Sample sizes are shown above each bar.

29 days prior to hatching (Figs. 2, 3). During the 4 wk prior to hatching and the 5 wk after hatching, 89% of females and 63% of males showed evidence of wing molt. Females were more likely to be molting during the early stages of incubation than were males (Fig. 2). Most males did not show signs of molt until after their young hatched. The primaries in molt stage were either P4 or P5 and sometimes both. In almost all cases, the same primaries were molting simultaneously on both wings. In some cases, secondaries (usually S4 or S5) were also molting. Data from 10 individuals in which molt status was recorded in consecutive years suggest that the timing of wing molt is

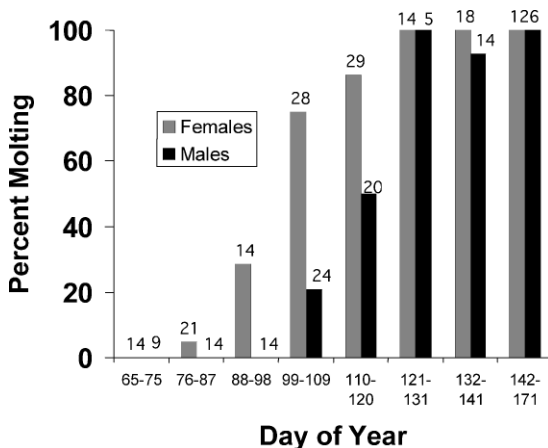


Figure 3. Percent of Prairie Falcons showing evidence of wing molt in relation to day of year. Sample sizes are shown above each bar.

similar each year. We recorded no evidence of tail molt during the nesting season.

DISCUSSION

We found two nonoverlapping distributions in several measurements of adult Prairie Falcons during the nesting season, which likely reflected different sexes. According to Snyder and Wiley (1976), Prairie Falcons are the third most sexually dimorphic raptor in North America. Only Sharp-shinned Hawks (*Accipiter striatus*) and Peregrine Falcons (*Falco peregrinus*) had higher dimorphism indices than Prairie Falcons in Snyder and Wiley's review. Our data suggest that Prairie Falcons may be slightly more dimorphic than Snyder and Wiley calculated (15.6 versus 15.4), and therefore, similar to Peregrine Falcons in their degree of sexual size dimorphism.

The only currently "accepted" technique for gender determination of Prairie Falcons is whether wing chord is greater or less than 320 mm (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1977). However, we recorded wing chords between 330–340 mm for birds we classified as males and females. Marzluff et al. (1991) found a bimodal distribution for toe-pad length in nestlings and suggested that falcons with toe-pads <86 mm be considered males and those with toe-pads >86 mm be considered females. Our results suggest that 83 mm would be a more appropriate criterion for distinguishing the sex of adults on the basis of toe-pad length. We suggest that criteria for sex determination of Prairie Falcons during the breeding season be expanded to include mass (greater or less than 700 g) and tail length (greater or less than 177 mm). Both of these characteristics are easy to measure and may be more accurate in classifying sex than wing chord, which shows some overlap among males and females. Measures of toe-pad and wing chord can be influenced by how much the investigator extends the toes or wing. Also, culmen and hallux lengths can be influenced by wear and age.

As in Eurasian Sparrowhawks (*Accipiter nisus*; Newton et al. 1983) and Eurasian Kestrels (Village 1990), female Prairie Falcon masses declined during the nesting season and showed more variation than male masses. Our results have implications for radiotelemetry studies. Researchers who are attaching transmitters to female falcons early in the nesting season should anticipate that females might lose 12% of mass by the end of the nesting season. Larger female masses during the early part of the nesting season probably represent energy reserves, which are necessary for egg laying and which buffer females from temporary food shortages during incubation (Newton et al. 1983). According to Village (1990), the normal equilibrium between energy intake and expenditure is altered during the breeding season because males expend energy capturing food they do not eat, and females eat food that they do not catch. Female Prairie Falcons reportedly do all nocturnal and most diurnal incubation (Kaiser 1986, Holthuijzen 1989). Males deliver almost all prey until

young are 1 wk old. Females deliver an increasing amount of prey as brood rearing progresses: nearly 40% of prey during the last half of brood-rearing (Kaiser 1986, Holthuijzen 1990). When females resume hunting, wing loading has decreased to a point where they can lift and carry prey more efficiently.

Prairie Falcons were similar to Eurasian Sparrowhawks in that females started molting soon after laying their eggs; onset of molt was later for males (Newton and Marquiss 1982). As in Eurasian Sparrowhawks, male Prairie Falcons "retained full wing efficiency while they were hunting to provision their incubating mates" (Newton and Marquiss 1982). Tucker (1991) showed that gliding performance of a Harris's Hawk (*Parabuteo unicinctus*) declined when missing primaries left gaps in the wing. Aerodynamic performance is particularly reduced when molt gaps occur in the middle of the wing (Hedenström and Sunada 1999), as with P4 and P5. Costs of molt include reduced flight efficiency, the energetic expense of feather synthesis, and the ability to thermoregulate. Males may delay molt because feather loss might hamper their ability to capture and carry prey when their mates are incubating (Village 1990). Alternatively, because energy expenditures are at a peak during incubation and early brood-rearing, they may be unable to allocate energy to feather synthesis until their mates share in hunting later in the nesting season (Village 1990). Our data confirm Enderson's (1964) finding that wing molt begins in spring with P4 and P5, but we found that molt in southwestern Idaho began much earlier than reported by Enderson. Mean hatching dates for Idaho Prairie Falcons are 3 wk earlier than for falcons nesting in Enderson's Colorado study area (Steenhof 1998), but molting in Idaho occurred at least 40 d earlier than reported by Enderson. Prairie Falcons that nest in the NCA feed on Piute ground squirrels (*Spermophilus mollis*), which are available for only a few months each year. Nesting chronology of Prairie Falcons in the NCA closely matches the chronology of the ground squirrel's annual cycle; peak of falcon hatching coincides with emergence of small, naïve juvenile ground squirrels (USDI 1996). During incubation, falcons feed primarily on large adult ground squirrels (\bar{x} = 201 g, N = 2853; USGS unpubl. data). Most male Prairie Falcons in the NCA did not begin molting until smaller, juvenile ground squirrels became available. The increasing percentage of molting males 1 wk after hatching also coincided with their decreasing role in providing food to their mate and their young. Females may begin molt earlier than males because it takes longer to grow their larger feathers. Growing two new feathers on each wing early in the nesting season may benefit females because a full complement of feathers that includes new ones would be beneficial during their post-nesting migration, which begins soon after nesting season ends (Steenhof et al. 2005). Molt and mass changes of breeding Prairie Falcons in the NCA appear to be timed to optimize energy allocation, as falcons exploit a seasonally abundant prey resource. It is not clear whether this

strategy is typical of Prairie Falcons throughout their range.

VARIACIONES EN EL DIMORFISMO DEL TAMAÑO, ESTADO DE LA MUDA Y PESO CORPORAL DE INDIVIDUOS DE *FALCO MEXICANUS* QUE NIDIFICAN EN EL ÁREA DE CONSERVACIÓN NACIONAL DE AVES DE PRESA SNAKE RIVER

RESUMEN.—Los adultos de *Falco mexicanus* capturados y medidos durante la estación reproductiva en el sudoeste de Idaho mostraron un alto nivel de dimorfismo sexual. El peso corporal y el largo de la cola pueden ser las mejores características para distinguir los sexos de *F. mexicanus* en el campo. El peso promedio de las hembras disminuyó significativamente desde el inicio de la incubación hasta la cría de los pichones, pero el peso de los machos no mostró cambios significativos durante el mismo período. El 63% de las hembras y el 34% de los machos estaban mudando las plumas del ala (P4 o P5) en el momento que fueron capturados. Las hembras presentaron mayor probabilidad de estar mudando que los machos durante los estadios tempranos de la incubación. La mayoría de los machos no mostró signos de muda hasta que eclosionaron sus pichones. Los cambios de muda y de peso de individuos reproductivos de *F. mexicanus* en el Área de Conservación Nacional de Aves de Presa de Snake River parecen estar sincronizados para optimizar el uso de la energía, ya que los halcones utilizan presas que son un recurso estacionalmente abundante.

[Traducción del equipo editorial]

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LITERATURE CITED

- BLOOM, P.H. 1987. Capturing and handling raptors. Pages 99–123 in B.G. Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [Eds.], Raptor management techniques manual. National Wildlife Federation, Washington, DC U.S.A.
- , J.L. HENCKEL, E.H. HENCKEL, J.K. SCHMUTZ, B. WOODBRIDGE, J.R. BRYAN, R.L. ANDERSON, P.J. DETRICH, T.L. MAECHTLE, J.O. MCKINLEY, M.D. MCCRARY, K. TITUS,

- AND P.F. SCHEMPF. 1992. The dho-gaza with Great Horned Owl lure: an analysis of its effectiveness in capturing raptors. *J. Raptor Res.* 26:167–178.
- BORTOLOTTI, G.R. 1984. Sexual size dimorphism and age-related size variation in Bald Eagles. *J. Wildl. Manage.* 48:72–81.
- BURNHAM, W. 1983. Artificial incubation of falcon eggs. *J. Wildl. Manage.* 47:158–168.
- ENDERSON, J.H. 1964. A study of the Prairie Falcon in the central Rocky Mountain region. *Auk* 81:332–352.
- ESPIE, R.H.M., P.C. JAMES, I.G. WARKENTIN, AND L.W. OLIPHANT. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). *Auk* 113:363–369.
- HEDENSTRÖM, A. AND S. SUNADA. 1999. On the aerodynamics of molt gaps in birds. *J. Exp. Biol.* 202:67–76.
- HOLTHUIJZEN, A.M.A. 1989. Behavior and productivity of nesting Prairie Falcons in relation to construction activities at Swan Falls Dam. Final report. Idaho Power Co., Boise, ID U.S.A.
- . 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. *Condor* 92:475–484.
- KAISER, T.J. 1986. Behavior and energetics of Prairie Falcons (*Falco mexicanus*) breeding in the western Mojave Desert. Ph.D. dissertation, University of California, Los Angeles, CA U.S.A.
- LEHMAN, R.N., K. STEENHOF, L.B. CARPENTER, AND M.N. KOCHERT. 2000. Turnover and dispersal of Prairie Falcons in southwestern Idaho. *J. Raptor Res.* 34:262–269.
- MARZLUFF, J.M., C. COODY, T.L. MAECHTLE, M. McFADZEN, T.C. MILES, L.S. SCHUECK, AND M. VEKASY. 1991. Influence of military training on the behavior of raptors in the Snake River Birds of Prey Area, 1991. Pages 37–95 in K. Steenhof and K. Sundberg [Eds.], *Snake River Birds of Prey Area research and monitoring annual report 1991*. U.S. Bureau of Land Management, Boise District, Boise, ID U.S.A.
- , B.A. KIMSEY, L.S. SCHUECK, M.E. McFADZEN., M.S. VEKASY, AND J.C. BEDNARZ. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. *Condor* 99:567–584.
- MORITSCH, M.Q. 1983. Photographic guide for aging nestling Prairie Falcons. USDI Bureau of Land Management, Boise, ID U.S.A.
- MUELLER, H.C., D.D. BERGER, AND G. ALLEZ. 1976. Age and sex variation in the size of goshawks. *Bird-Banding* 47:310–318.
- NEWTON, I. AND M. MARQUISS. 1982. Molt in the sparrowhawk. *Ardea* 70:163–172.
- , ———, AND A. VILLAGE. 1983. Weights, breeding and survival in European Sparrowhawks. *Auk* 100:344–354.
- PENNYCUICK, C.J. 1999. Measuring birds' wings for flight performance calculations, 2nd Ed. Boundary Layer Publications, Bristol, England.
- PYLE, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA U.S.A.
- SCHMUTZ, J.K. 1992. Molt of flight feathers in Ferruginous and Swainson's hawks. *J. Raptor Res.* 26:124–135.
- AND S.M. SCHMUTZ. 1975. Primary molt in *Circus cyaneus* in relation to nest brood events. *Auk* 92:105–110.
- SNYDER, N.F.R. AND J.E. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.* 20:1–98.
- STEENHOF, K. 1998. Prairie Falcon *Falco mexicanus*. In A. Poole and F. Gill [Eds.], *The Birds of North America*, No. 346. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC U.S.A.
- , M.R. FULLER, M.N. KOCHERT, AND K.K. BATES. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. *Condor* 107: 481–496.
- , M.N. KOCHERT, L.B. CARPENTER, AND R.N. LEHMAN. 1999. Long-term Prairie Falcon population changes in relation to prey abundance, weather, land uses, and habitat conditions. *Condor* 101:28–41.
- TUCKER, V.A. 1991. The effect of molting on the gliding performance of a Harris's Hawk. *Auk* 108:108–113.
- U.S. FISH AND WILDLIFE SERVICE AND CANADIAN WILDLIFE SERVICE. 1977. North American bird banding manual, Vol. 2, Bird Banding Techniques. Part 6, No. 355.0. U.S. Fish and Wildlife Service, Washington, DC U.S.A., and Canadian Wildlife Service, Ottawa, Ontario, Canada.
- U.S. DEPARTMENT OF THE INTERIOR. 1996. Effects of military training and fire in the Snake River Birds of Prey National Conservation Area. U.S. Geological Survey, Biological Resource Division, Snake River Field Station, Boise, ID U.S.A.
- VILLAGE, A. 1990. The Kestrel. T. and A.D. Poyser, Ltd., London, England.

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